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A Review of the Valbyteuthidae And an Evaluation of its Relationship With the Chiroteuthidae (Cephalopoda: Oegopsida) ¹

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Joubin (1931) described from the Bay of Panama an unusual squid, *Valbyteuthis danae*, which possessed such distinctive characters that he placed it in a new family. He aligned this family, the Valbyteuthidae, with the Chiroteuthidae and Brachioteuthidae. Since the original description, no additional specimens of this family have been reported in the literature; Robson (1948, p. 127), however, briefly described, as *Chiroteuthis*, a small specimen that appears to be *Valbyteuthis*. Thiele listed the Valbyteuthidae in his systematic handbook (1935).

The extensive cephalopod collections currently being studied at the Institute of Marine Science of the University of Miami contain a number of specimens of *Valbyteuthis*. This material was captured over a broad geographic area including the type-locality. Examination of the material indicates that *Valbyteuthis* does not warrant inclusion in a separate family, a fact that necessitates a re-evaluation of the systematic position of the group.

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The original description is based upon a specimen captured in the Bay of Panama during the *Dana* Expedition (1920-1922). The present material includes *Dana* specimens, one of which was taken at the third station following the capture of Joubin's holotype. In addition, material is utilized from the following sources: United States Antarctic Research Program, USNS *Eltanin*; Inter-American Tropical Tuna Commission, M/V *Shoyo Maru*; Woods Hole Oceanographic Institute, R/V *Chain*; and University of Southern California, R/V *Velero* iv. The authors are grateful to Dr. E. Bertelsen of the Carlsburg Foundation, the U.S. Antarctic Research Program of the National Science Foundation, Dr. Klawe of the Inter-American Tropical Tuna Commission, Dr. R. H. Backus of Woods Hole Oceanographic Institute, and Mr. R. Lavenberg of the University of Southern California for making these specimens available for study.

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Family CHIOTEUTHIDAE Gray

VALBYTEUTHIDAE Joubin, 1931, p. 188.—Thiele, 1935, p. 971.

Valbyteuthis Joubin

Valbyteuthis Joubin, 1931, p. 188.—Thiele, 1935, p. 971.—Young and Roper, in press.

Chiroteuthis.—Robson, 1948, p. 127.

DIAGNOSIS.—A chiroteuthid with elongate ventral arms, oval funnel-mantle locking apparatus. Antitragus present, tragus absent. Short, compact tentacular club with suckers in four rows. Club suckers on short stalks. Broad, round, subterminal fins; length 60 percent of width. Photophores absent. Funnel valve absent.

The material examined is as follows:

vessel and station no.	location	<i>mantle</i> length (mm)	<i>estimated</i> depth of capture (m)
<i>Eltanin</i> 34	07°45'N 81°37'W	47	683
<i>Eltanin</i> 52	16°30'S 74°36'W	35	1162
<i>Eltanin</i> 741	40°16'S 78°18'W	31	2635
<i>Eltanin</i> 743	33°18'S 72°27'W	30	1830
<i>Dana</i> 3980 IX	23°26'S 03°57'E	38	1500
<i>Dana</i> 1206 v	06°40'N 80°47'W	34	1250
<i>Dana</i> 1370 XIII	36°36'N 26°14'W	31	1500
<i>Dana</i> 1171 XII	08°19'N 44°35'W	21	1000
<i>Dana</i> 1203 XII	07°30'N 79°19'W	25	1250
<i>Dana</i> 1208 VII	06°48'N 80°33'W	19	1000
<i>Dana</i> 4003 IV	08°26'S 15°11'W	24	1500
<i>Dana</i> 4014 III	28°09'N 15°19'W	11	450
<i>Dana</i> 4158 XIV	46°28'N 08°01'W	12	2000

essel and station no.	location	mantle length (m)	estimated depth of capture (m)
Chain 35-958	09°17'N 49°04'W	55	530
Shoyo Maru 8	39°12'S 106°48'W	35, 34, 33	<i>Alepisaurus</i> stomach
Shoyo Maru 7	40°09'S 109°38'W	34	<i>Alepisaurus</i> or alba- core stomach
Scot 77	14°12'N 92°47'W	15	300
Velero IV-10265	33°18'N 118°40'W	33, 26, 25	1200

Valbyteuthis danae Joubin

Valbyteuthis danae Joubin, 1931, p. 188.—Thiele, 1935, p. 971.

DESCRIPTION.—This description is based only upon material captured in the region of the type-locality (Elt. 34; *Dana* 1206 v, 1203 xii, 1208 vii). Measurements are given on page 5. The mantle is short and broad; the muscular portion tapers rapidly posteriorly and terminates beneath the anterior third of the fins. Only the integument continues posteriorly over the gladius. The mantle wall is thin but muscular (pl. 2B).

Fins are huge and extremely muscular; their length is about 50 percent of the mantle length and their width is about 80-85 percent of the mantle length. The anterior lobes are attached to the dorso-lateral sides of the mantle. The attached borders of the anterior fin lobes are clearly visible beneath the integument and form a broad V. The posterior border of each fin is indented slightly at the midline; the lateral margin is semicircular in outline (pl. 2A).

The gladius has a long, narrow, extremely delicate rhachis. The short, thin vane arises abruptly near the anterior level of the fins, folds rapidly ventrally, and fuses in the midline to form a long, slender conus. The walls of the conus are much heavier than the anterior portion of the gladius. The conus is rectangular in cross-section and is broken just posterior to the fins. The terminal portion has been lost in all specimens; it is apparent, however, from the large diameter and heavy construction of the conus that *Valbyteuthis* possesses a long tail (pl. 2c).

The funnel is large and narrow and reaches the level of the middle of the eyes. The funnel component of the locking apparatus is oval and deeply concave, particularly at the posterior end, where the depression tends to undercut the lateral margin. A distinct antitragus is present on the posterior wall of the funnel component. The mantle component is [human] nose shaped, with the tip directed posteriorly. The component also curves laterally to conform to the deep lateral depression of the funnel component. A small indentation that locks with the antitragus is located beneath the tip at the posterior end of the mantle component (pl. 4A,B).

The dorsal member of the funnel organ is broadly triangular in outline, with only a small posterior indentation. A spatulate papilla

arises from the anterior apex. The ventral members are large and oval. No trace of a funnel valve exists (pl. 4c).

The head is elongate; toward the anterior end it bears large protruding eyes that are directed slightly forward. The "olfactory" organs are situated posterior to the eyes on long, slender stalks. Nuchal crest and nuchal folds are lacking. Two heavy, muscular bridles extend from the cephalic cartilage along the ventral surface of the head and attach to the dorsolateral sides of the tubular portion of the funnel. The cephalic vein lies close to the surface in the midline between the bridles (pls. 1c, 2b).

The arms are weak and slender and arranged in the order $4.3=2.1$. The dorsal three pairs of arms bear biserially arranged suckers throughout their length. In some specimens, the ventral row of suckers of these arms possesses two to four moderately enlarged suckers located about two-thirds of the distance along the length of the arm. Probably this represents a sexual dimorphism, but because the specimens are insufficiently developed, the sexes cannot be determined in all cases. The sucker stalks are short and arise from large, conical bases. The chitinous rings are large but possess very small apertures that bear approximately 7-10 (average 8) short, broad, truncate teeth that are separate along the distal half of the margin. In the proximal half, the teeth are fused, giving a smooth margin that becomes slightly scalloped laterally (pl. 4K-N). The dorsal three pairs of arms appear to bear low keels, particularly along the distal portions. The arms, however, have been injured so that the true nature of the keels is difficult to determine. Protective membranes are developed weakly and, although they are not supported by distinct trabeculae, their margins are scalloped.

The ventral arms are extremely long, slender, and fragile and have large lateral membranes that extend their full length. The suckers originate in two rows at the base of each ventral arm but gradually tend to converge into a single row near the middle of the arm. These suckers are extremely small and decrease in size toward the middle portion of the arm, where they disappear, leaving the distal half of the arm naked. No protective membranes or trabeculae occur on arms iv.

Tentacles are long and slender; they bear very short, simple clubs. Keels are not apparent. The protective membranes form an indistinct ridge and trabeculae are indistinguishable (pl. 1d). The carpal area bears approximately four to five small suckers that alternate in two longitudinal rows. The outer chitinous rings of these suckers are narrow bands. The inner rings have three superimposed rows of small, rounded knobs; the outer row bears about 15 knobs. The smaller knobs of the inner rows alternate with those of the outer row

(pl. 4H). The suckers of the manus and dactylus are arranged in four uniform, longitudinal rows, except at the tip, where only one or two suckers remain. The suckers have broad, flat outer chitinous rings. The inner rings have very small apertures and lack dentition (pl. 4I, o).

The buccal membrane possesses seven buccal lappets. The buccal membrane connectives attach dorsally to arm pairs one and two and ventrally to arm pairs three and four. The oral surface of the buccal membrane is covered with distinct, closely set longitudinal ridges and grooves.

A few irregularly scattered, brown chromatophores are present on the mantle, fins, head, and arms.

The beaks are illustrated on plate 4, figures D-F. The rostrum of the upper mandible is short and has a sharply pointed tip; the palatine lamella is short and broad. The rostrum of the lower beak is short and triangular and has dorsolateral ridges on the hood. A weak lateral ridge is present on the gular lamella.

The radula consists of seven rows of teeth in a transverse series. The rhachidian tooth has a very slender, elongate, median cusp and two lateral cusps that frequently bear a small medial bump. The first lateral tooth has a long, medial cusp and two small lateral cusps; the smaller and more medial of these is somewhat variable in size but provides the first lateral tooth with a distinctive and unusual feature. The second lateral tooth has a broad base and bears a single, long, slender cusp. The lateralmost tooth has an extremely elongate, curved cusp. Marginal plaques are lacking in *Valbyteuthis* (pl. 4G).

Measurements in mm of two specimens of *Valbyteuthis danae* Joubin from the region of the type-locality (Bay of Panama) are as follows:

	<i>Eltanin 34</i>		<i>Dana 1296 v</i>	
sex	male		?	
mantle length	47		34	
mantle width	16		12	
head length	21		14	
head width	16		12	
fin length	25		17	
fin width	40		29	
arm length	right	left	right	left
I	20	21	8*	13
II	22	25	14	15
III	—	26	17	15*
IV	43	37*	25	27
tentacle length	81	78	36	37
club length	7½	7	4	4½

*Marks indicate that tip of arm is missing.

DISTRIBUTION.—Figure 1 shows the distribution of the genus *Valbyteuthis*, which was recorded previously only from the type-locality, 07°30'N, 79°19'W. The genus is now known to occur throughout the Atlantic Ocean from about 25°S to 46°N and in the Eastern Pacific Ocean from about 40°S to 35°N. The longitudinal range is from 04°E to 120°W. We do not suggest that these are the distributional limits of the genus.

The distributional map refers to the genus *Valbyteuthis* and not to *V. danae*. It is evident from our specimens that at least two species occur other than *V. danae*, but formal recognition of them must wait until further material becomes available.

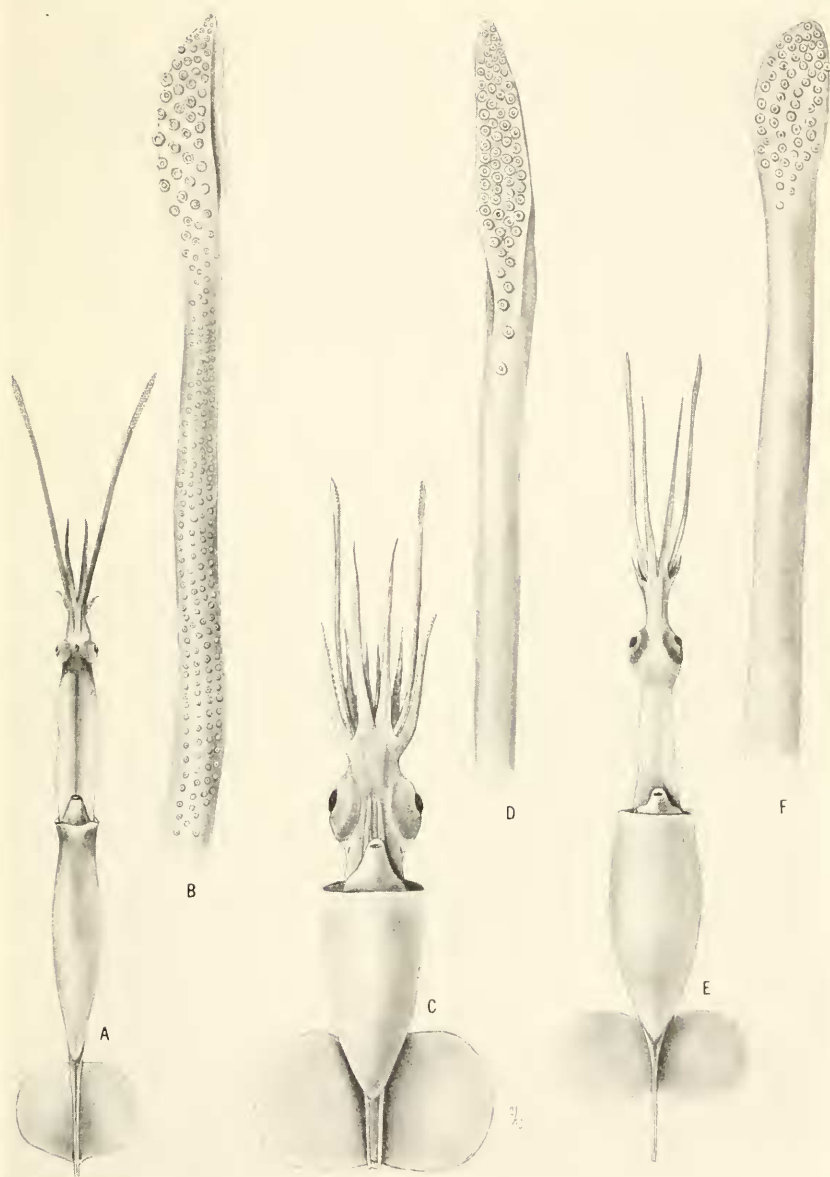
Discussion

On the basis of the material available to us, it is possible to re-evaluate the status of the Valbyteuthidae. Numerous characteristic features are possessed by *Valbyteuthis* that clearly demand that its familial ranking be submerged and that the genus be placed in the Chiroteuthidae sensu stricto. The most important of these features are discussed below.

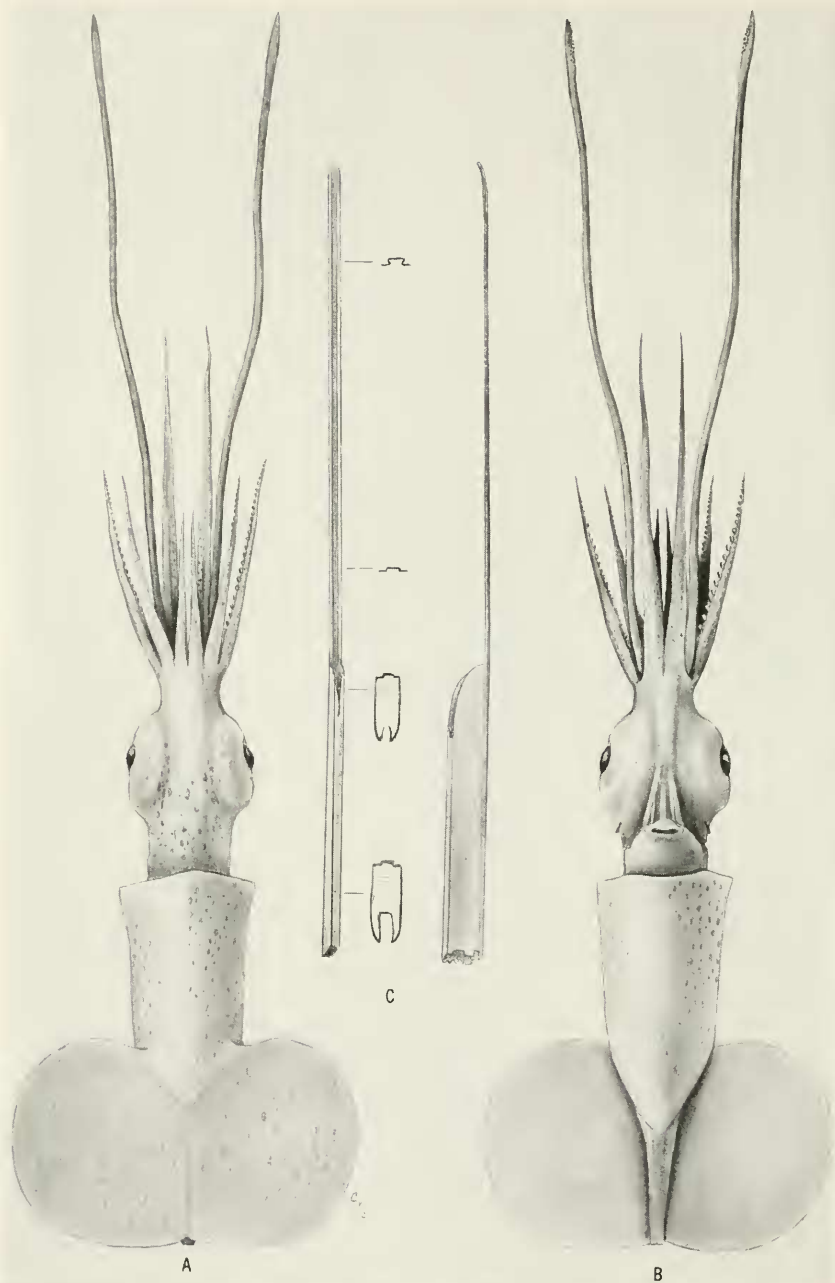
The connectives of the buccal membrane of *Valbyteuthis* are attached to the dorsal sides of arms one and two and to the ventral sides of arms three and four. The gladius consists of a long, narrow rhachis and a vane that folds ventrally until the edges fuse in the ventral midline to form a long, slender conus. These features align *Valbyteuthis* with the Chiroteuthidae and a number of related families (see Young and Roper, in press, for a more detailed discussion).

The closely related families Mastigoteuthidae and Chiroteuthidae possess distinctive funnel-mantle locking apparatuses. The funnel components of these structures are oval and bear one or two protuberances (tragus and antitragus) that give them an ear-shaped appearance. This characteristic locking mechanism is not found in other families. Joubin (1931) described and illustrated the locking apparatus of *Valbyteuthis* as oval but without protuberances and stated that it was not ear shaped. Our specimens, including those from the type-locality, possess a well-developed antitragus on the posterior wall of the funnel component. Although this differs from *Chiroteuthis* by lacking a tragus, it unquestionably falls within the chiroteuthid-mastigoteuthid pattern. Joubin's failure to observe this structure is partly responsible for his incorrect systematic placement of *Valbyteuthis*.

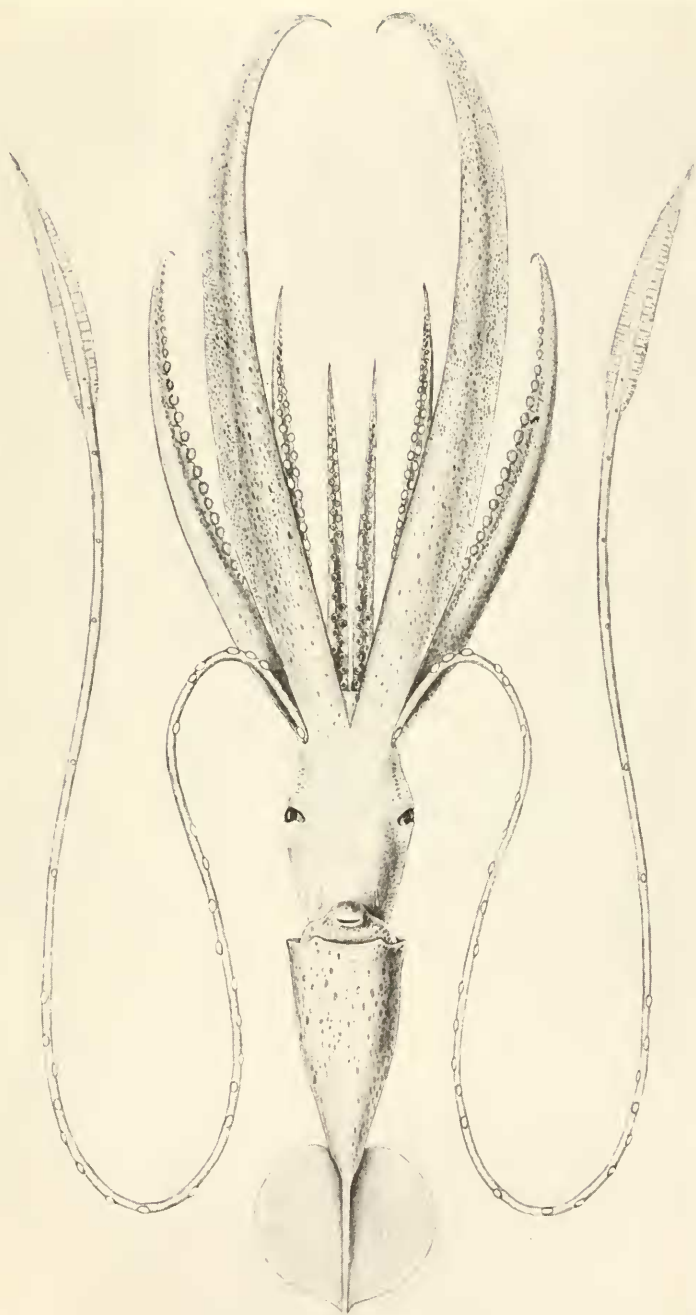
Probably the most distinctive feature of *Valbyteuthis* that could be used to substantiate its position in an independent family is the peculiar structure of the tentacular clubs. These clubs are unlike those found in any adult chiroteuthid. They are, however, nearly



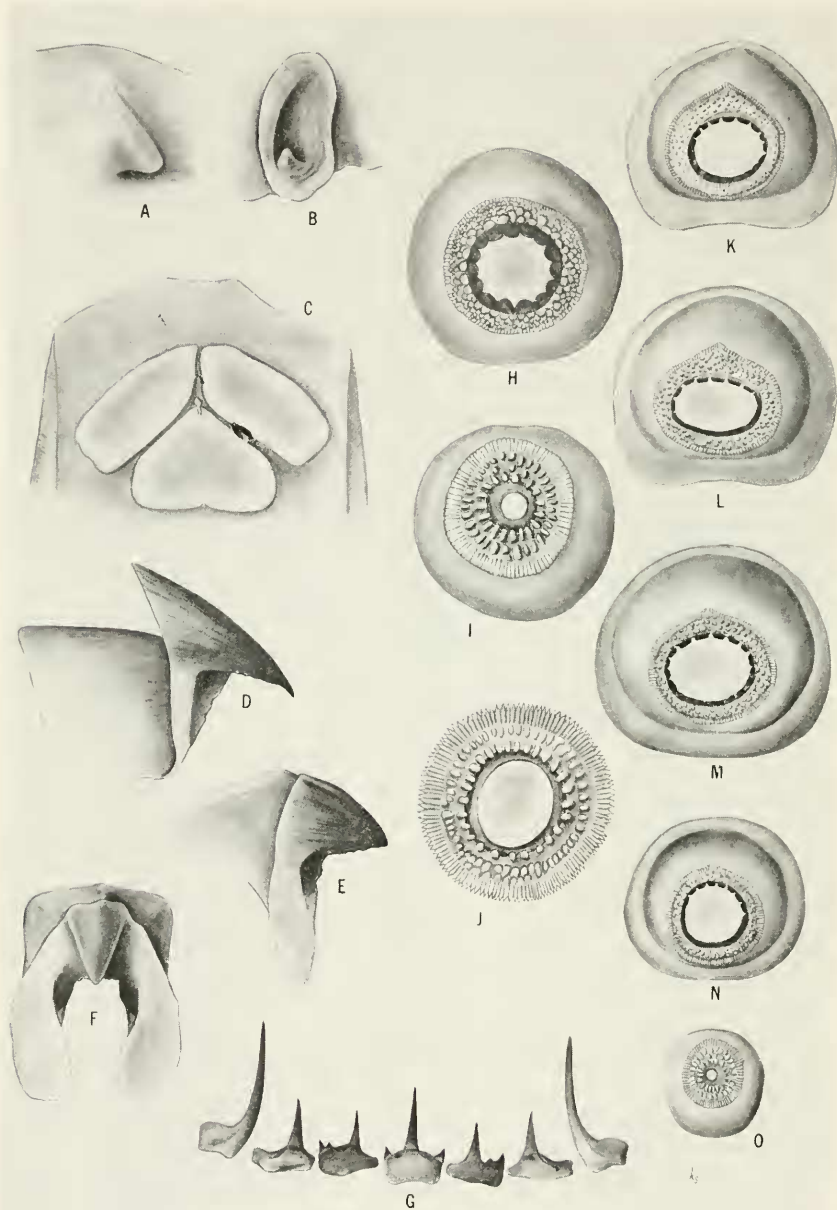
Chiroteuthis: A, "doratopsis" stage, 32 mm mantle length (ML) (modified from Pfeffer, 1912, pl. 46: fig. 4); B, "doratopsis"-type tentacle showing larval club distally and developing adult club on stalk, 28 mm ML, *Dana* 1157 II. *Valbyteuthis danae*: C, ventral view, 34 mm ML, *Dana* 1206 v; D, adult tentacular club, 47 mm ML, *Elt.* 34. *Valbyteuthis* species: E, ventral view of larva, 15 mm ML, *Scot* 77; F, larval tentacular club, 15 mm ML, *Scot* 77.



Valbyeuthis danae, 47 mm ML, *El.* 34: A, dorsal view; B, ventral view; C, ventral and lateral views of gadius with cross sections.



Chiroteuthis species, 63 mm ML, *Velero* 9349: ventral view (this species has a "doratopsis"-type larva).



Falbyteuthis danae, 47 mm ML, *Elt.* 34: A, B, mantle and funnel components of locking apparatus; D-F, upper and lower mandibles; G, radula; H, sucker from carpus; I, sucker from manus enlarged; K-N, suckers from arms I-IV; O, sucker from manus (K-O = identical enlargement). 35 mm ML, *Elt.* 52: C, funnel organ. *Chiroteuthis*, "dorstopis"-type larva, 28 mm ML, *Dana* 1157 H: J, sucker from manus.

identical with the early larval clubs of *Chiroteuthis*, the predominant genus of the family. The adult *Chiroteuthis* club begins to develop in the larval stage along the tentacular stalk proximal to the primary larval club. The primary larval club is eliminated upon metamorphosis either by resorption or autotomy (pers. observ.). The striking similarity of clubs of *Valbyteuthis* and early larval *Chiroteuthis* is apparent in the illustrations on plate 1B, D, and F, and indicates the close relationship of the two genera.

Further relationship between these genera is suggested by the close resemblance of the extremely long, weak, ventral arms; they

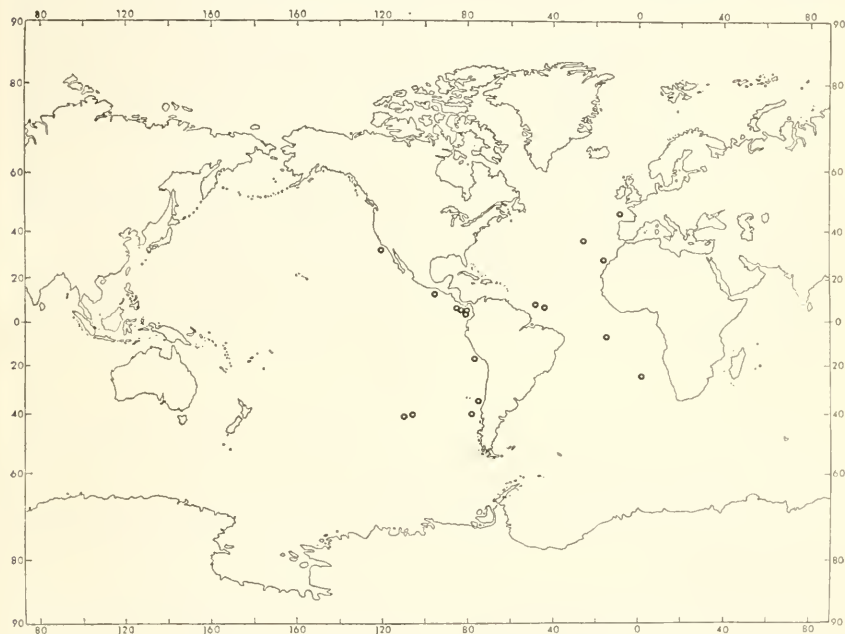


FIGURE 1.—Geographic distribution of *Valbyteuthis*.

bear small suckers that are aligned nearly in a single row, and they possess very large lateral membranes. These features give the arms a very distinctive appearance. The characteristic lateral membranes were not mentioned in Joubin's description and did not appear in his illustration, probably due to the poor condition of his specimen.

Although the adults of the two genera appear to differ considerably in overall appearance (pls. 2A, B, 3), general similarities do exist. In addition to the characteristics already mentioned, both groups have elongate heads, oval fins, and similar arm formulae.

The larval stages of *Valbyteuthis* and *Chiroteuthis* (especially the "doratopsis" type) show even greater similarities, particularly in the following details: very elongate head, long fourth arms, relatively

short tentacles, simple clubs, long tail, superficial position of cephalic vein and funnel bridles, spindle-shaped liver, and absence of photophores (pl. 1A, E). The two larval forms can be distinguished only by close examination. As the "doratopsis" develops, the adult club begins to form on the tentacular stalk, light organs appear on the viscera, eyes, ventral arms, and tentacles, and the head begins to shorten. At metamorphosis, the tentacles become greatly elongated; the early larval club is lost, and the body proportions change.

As the larval *Valbyteuthis* develops, only a few changes occur, of which the shortening of the head is the most noticeable. Even though our large specimens are not sexually mature, no evidence of an impending metamorphosis exists, and it is clear that these specimens represent the adult form and are not oversized larvae. Therefore, while *Chiroteuthis* undergoes considerable change during development, *Valbyteuthis* remains approximately at the "doratopsis" stage.

The above discussion reveals that *Valbyteuthis* closely resembles *Chiroteuthis*. The similarities are particularly strong between *Valbyteuthis* and the larval "doratopsis" stage of *Chiroteuthis*. Therefore, although these two genera are clearly distinct, it is not possible to maintain the more recently described family, the Valbyteuthidae, as a distinct taxon, and it is placed herein in the synonymy of the family Chiroteuthidae.

Summary

Valbyteuthis danae Joubin, 1931 is redescribed based on *Dana* and *Eltanin* material from the type-locality.

The known distribution of the genus *Valbyteuthis* extends in the Eastern Pacific from 40° S to 35° N and throughout the Atlantic from 25° S to 46° N.

The family Valbyteuthidae is submerged in the family Chiroteuthidae, primarily on the basis of the similarities between *Valbyteuthis* and certain larval chiroteuthids ("doratopsis" type). *Valbyteuthis* remains a distinct genus.

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